NESTING BEHAVIOR OF THE POO-ULI

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ABSTRACT.—We describe two sequential nestings of a pair of Poo-uli (*Melamprosops phaeosoma*), a Hawaiian honeycreeper nearing extinction. Similarities to nesting of most other honeycreepers included: nest site in ohia lehua (*Metrosideros polymorpha* Gaud.) canopy; breeding in March through June; monogamous breeding system with the putative male helping build the nest, feeding the putative female throughout each nesting event, and feeding the chicks, but not incubating or brooding; and complete nest sanitation. Notable differences were the paucity of songs and calls by the parents and inclusion of snails in the diet of nestlings. Clutch size was probably two eggs for both nests. High winds, rain, or both influenced parental behavior: the female stayed longer on the nest and took shorter recesses in poor weather. Weather did not affect rates at which the male fed the female on the nest; however, the feeding rate increased from the egg to the chick stage probably because food was passed on to the chicks. At nest #2, parents fed young chicks (<14 days old) more often in good than in poor weather; data were insufficient for old chicks. Weather is usually poor throughout the year in the relictual range of the Poo-uli and is likely to impact nesting success. The first nest failed in poor weather. The second fledged a single young 21 days old. Diet of nestlings appeared to consist of a higher proportion of insect larvae than that of older birds, which are reported to eat mostly snails. *Received 12 Dec. 1994, accepted 27 May, 1996.*

Few endangered birds are closer to extinction than the Poo-uli (*Melamprosops phaeosoma*), a monotypic species and genus of Hawaiian honeycreeper (Fringillidae; Drepanidini). Since its discovery on Haleakala Volcano, Maui Island in 1973 (Casey and Jacobi 1974), the Poo-uli population has fallen from several hundred to fewer than 10 birds today, and it is extinct at the type locality (Scott et al. 1986; Engilis 1990; Mountainspring et al. 1990; J. Simon and M. Reynolds, pers. comm.).

Why is the Poo-uli disappearing? Past research has been sporadic and underfunded; consequently the life history and population ecology of the bird are poorly understood. Field work has also been hampered by logistical difficulties, inhospitable conditions, and the bird's low population density and lack of vocal activity. Nevertheless, scant data (Casey and Jacobi 1974, Baldwin and Casey 1983, Engilis 1990, Mountainspring et

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al. 1990) and conjecture based upon biology of other honeycreepers (Kepler et al. 1984; Scott et al. 1986; van Riper et al. 1986; Engilis 1990; Mountainspring et al. 1990; Atkinson et al. 1995) implicate habitat damage by feral pigs (*Sus scrofa*), predation by and competition with nonnative small mammals, increased risk to avian disease below 1800 m elevation, and the untested hypothesis that the bird's molluscan prey base is also dwindling. The poo-uli's substrate-restricted foraging for arthropods and molluscs in bark and epiphytes (Mountainspring et al. 1990) implies ecological specialization vulnerable to environmental change brought about by the invasion of non-native organisms. So far, recovery efforts begun in 1990 have focused not on the poo-uli, but on successful habitat restoration through pig removal and exclusion. Recently, the National Biological Service, funded and otherwise supported by other agencies (see Acknowledgments), initiated a program for research and restoration of the Poo-uli.

In 1985–1986, Kepler and Engilis studied aspects of the ecology of endangered Maui birds, including the Poo-uli (Mountainspring et al. 1990) at Hanawi Natural Area Reserve. In 1986, they discovered and monitored two active nests of a pair of Poo-uli. Our purpose is to describe events at these nests in as much detail as possible, because (1) this is the only information on Poo-uli reproduction, (2) recovery efforts, in the field and in captivity, will benefit from knowledge of the natural history of the species, and (3) the Poo-uli may go extinct, leaving no further record. We compare behavior of the Poo-uli with that of other Hawaiian honeycreepers and mainland cardueline finches, from which the honeycreepers are descended (James and Olson 1991). We also discuss how this information may help the species' survival.

STUDY SITE AND METHODS

The two nests were within about 30 m of each other along a small, eastern tributary ravine of the east fork of Hanawi Stream at 1800 m elevation. Nest #1 was situated on a small ridge crest, more exposed to prevailing trade winds than nest #2, which was on the east flank of the same ridge about 15 m above the ravine floor. Both were within 100 m of a headwall of the Hanawi gulch. Vegetation at the site was Mixed Shrub Montane Wet Forest (Jacobi 1989) with mean canopy height of 13 m and crown cover averaging 60% and dominated by ohia lehua (*Metrosideros polymorpha* Gaud.) (Mountainspring et al. 1990). Damage to vegetation by feral pigs appeared slight, with the under story largely intact. Rainfall, brought year-round predominantly by NE trade winds, was estimated to exceed 3 m per annum.

Nest #1 was built in a canopy ohia lehua 15 m tall. Vegetation surrounding the nest tree included (1) a subcanopy kolea tree (*Myrsine* sp.) and pukiawe shrub (*Styphelia tameiameiae* [Cham. & Schlechtend.] F. v. Muell.) where the male often fed the female, and (2) a dense understory of shrubs and ferns used as cover by the birds when approaching or leaving the nest area. The nest was located in a secondary, horizontal branch in the lower crown, 8 m

TABLE 1

DATES OF OBSERVATION AND NEST STAGES

	Dates	Stage
Nest #1	5–6 March	Nest construction, courtship
	17–20 March	Eggs
	24–26 March	Eggs hatch 25 March; nestling
	31 March to 3 April	Nestling; first seen April 2
	7 April	Nestling
		Nest fails 8–14 April
Nest #2	16 April	Nest construction
	9–14 May	Eggs hatch 11, 13 May; nestlings
	19–22 May	Nestlings
	29–31 May	Nestlings, one fledges on 31 May
	1 June	Fledgling

above ground, and was incorporated into live twigs and small branchlets a few cm below live foliage. The nest site was exposed to some direct sunlight in the morning and was sheltered from trade winds, but it swayed in an arc of ca 1 m in SE winds >13 km·h^{-1}. The globular, open cup nest was composed of sticks, mosses, and plant fiber (Engilis et al. 1996). Two other, inactive and unidentified nests occupied foliage above and below on the same branch. During nest construction, the male infrequently visited a fourth, triangular nest 4 m up in a 5-m ohia lehua sapling within 10 m of the nest tree. Based on the construction and location of this nest, we believe it was built by a non-native Red-billed Leiothrix (*Leiothrix lutea*).

Nest #2 was also built in an ohia lehua tree surrounded by similar vegetation. Nearby pukiawe and kanawao (*Broussaisia arguta* Gaud.) shrubs provided nest material. This nest was placed in the tree in a position very similar to nest #1. The nest was only 8 m above ground and sheltered from NE trades, being situated in the SE (140°), uphill portion of the crown, and 5–10 m lower than the crowns of nearby ohia lehua. It was, however, exposed to SE winds which caused the nest branch to sway 1–2 m. No other nests were noted in the tree.

Only two Poo-uli were observed tending the nests. These care-givers, likely the same two birds at both nests, were recognized by plumage characters (Engilis et al. 1996). We assume the brightly colored bird was the male and the drab bird was the female. Viewed closely, neither showed lesions of active or past infection from avian pox that might have influenced their behavior.

We studied both Poo-uli nests for periods of one to five days, from nest construction until fledging or failure (Table 1). We observed Poo-uli at the nests from a distance of 40 m (nest #1) and 15 m (nest #2) through binoculars, spotting telescope (Bausch & Lomb 30×, nest #1) or Questar telescope (80×, nest #2) from under a tarp shelter. A creek separated observers from both nest trees, and when flowing vigorously it prevented us from hearing Poo-uli vocalizations, especially at the more distant nest #1. On most days, weather permitting, observers watched the nest continuously from 08:30 to 17:00 (all times are Hawaii Aleutian Times). We did not approach the nest trees while nests were active. Our presence did not appear to influence the birds' behavior at nest #1, but may have done so at the closer nest #2 (see below). From the observation points, we could usually view parental

behavior at the nests, but we could not see the nest contents until the nestlings were old enough to reach above the nest rim. We recorded: duration of behaviors at the nest to the nearest 10 sec, vocalizations, and feedings and other behaviors off the nest. We mapped the birds' movements to and from the nest.

At times, heavy rain or fog prevented accurate observation; these data were omitted from analyses. We estimated heights and distances to the nearest meter. We recorded percent cloud cover, rain scores (0 = none; 1 = mist; 2 = drizzle; 3 = light rain; 4 = downpour), and wind scores by the Beaufort scale. Once inactive, both nests were collected and deposited at the B. P. Bishop Museum, Honolulu (Engilis et al. 1996).

The Questar enabled us to identify some prey items brought to nest #2. We identified prey items as (1) caterpillars, for larvae colored other than white or pink; (2) pale larvae, for larvae colored white or pinkish, which likely were bark-dwelling coleoptera or lepidoptera; (3) beetles; (4) succineid snails (Succineidae); and (5) snails, for unidentified snails. Mountainspring et al. (1990) described foraging observations in vicinity of the nests.

We assigned observations to the incubation stage at nest #1 prior to 12:00 on 25 March and at nest #2 prior to 10:00 on 11 May; observations afterwards were assigned to the nestling stage. We categorized nestlings as young (<14 days) or old, based on the assumption that they were partly feathered, thermoregulating, and required less brooding by the parents at about 14 days age or older.

Time on the nest is the length of the visit to the nest; time off is the time from when the bird left the nest until it returned. Preliminary models using stepwise linear regression indicated that both wind and rain significantly affected time spent by the female on and off the nest. We created a combined weather variable that was coded as "poor" whenever winds exceeded 8 km·h^{-1} (Beaufort scale 2) or rain occurred (rain score >1) or both; otherwise, we coded weather as "good." The models also showed that nest number significantly affected time spent by the female on and off the nest, being longer for both at nest #2. Nearness of observers to nest #2 may have caused the female to hesitate leaving or returning to the nest. Consequently we analyzed nests separately for time spent by the female on and off the nest.

We compared rates of the male feeding the female at both nests combined and of parents feeding chicks at nest #2 (better visibility) using a test of comparison for two Poisson processes (Cox and Lewis 1978:225). Sample units were daily rates calculated separately for good and poor weather. Values of $P < 0.05$ were considered statistically significant.

RESULTS

Behavior

Nestbuilding.—Nest #1 was under final construction by one or both Poo-uli when discovered and first observed at 13:15–16:37 and 07:24–14:00 on 5 and 6 March, respectively. At that time, we did not record observations systematically. In the vicinity of the nest tree, the birds moved through the subcanopy of the forest at 5–12 m. They were exceptionally active for Poo-uli, moving quickly in the subcanopy, pausing at times to preen, forage or gather nest material such as moss from ohia lehua branches. When arriving in the nest tree, the birds flew quickly to the nest; when leaving, they often dropped vertically from the nest, dashing away above the undergrowth, then ascending trees distant from the nest. Both birds visited the nest with about equal frequency; however, we

did not determine if one or both performed nest construction. The male was observed singing repeatedly at and near the nest and while courting the female. Dense fog frustrated further observation on the second day. Once incubation began, we did not observe either parent taking building materials to the nest and assume that nest construction had ceased.

Nest #2 was also under final construction when discovered on 16 April. At nest site #1 at 12:10–16:00 on 14 April, we detected the male and female foraging and giving whistles and chit-chit calls 18 times, but did not hear song or observe nest-building. The pair was associated tightly, and we observed courtship feeding. We again visited the site at 10:55–14:50 on 16 April and observed the Poo-uli carrying material to a new nest at 12:00–13:24. Though both parents were present, the female was only once seen carrying material to the nest (moss collected near the ground), while the male was seen carrying material to the nest nine times (six times with twigs and three with moss). Twigs were collected three times from a pukiawe shrub, and moss was gathered three times, <1 m from the ground, in a kanawao shrub. We did not see either bird actually build the nest. The pair was silent during construction of this nest. Once incubation began, we observed the female add new material to either nest only once.

Courtship.—We observed courtship during nest-building only at nest #1, at 13:45–13:50 on 6 March. The male was detected singing and displaying to the female 12 m up in a 15 m ohia lehua tree distant from the nest. While the female stood still, the male circled her, wing-flicked, and delivered six songs in about 30 sec. The female then flew into the nest tree, with the male following and singing in flight. The female moved close to the nest; the male joined her and continued circling and singing eight songs in about 30 sec. The female then returned to her previous location in the distant tree, the male following and singing. Singing and chasing continued, screened from view.

Egg stage.—We observed nest #1 for 24.3 h in six days and nest #2 for 11.5 h in three days during the egg stage. At nest #1, egg(s) were laid either during 8–17 March (by 18 March the female incubated continuously) or on about 10 March, assuming an incubation period of 16 days and hatch date of 25 March. At nest #2, eggs were laid on about 26 and 27 April, assuming hatch dates of 11 and 13 May (see below). Laying of the second clutch followed 13–19 days after failure of the preceding brood. Clutch size was not determined but is assumed to be two, because at nest #1 we saw only one nestling and watched the female eating an egg, nest #2 contained two chicks, and when collected the nests contained neither remains of other eggs nor chicks.

Only the female incubated at both nests. Behaviors of the incubating female included inactivity, shifting position in the nest, breast pumping motions as she settled on eggs, preening, adjusting nest material, accepting food from the male, and manipulating objects inside the nest (probably turning the egg). She was also observed resting with eyes closed for a few seconds on nest #2 during the day. The incubating female crouched low in the nest with her head tilted upward so that her eyes peered just over the rim of the nest; at times she crouched so low that she was not visible. Occasionally, she would turn and face a different direction. Both she and her mate approached and left the nest tree quickly and deliberately from several favorite routes. They usually arrived at the nest by flying first into the nest tree, then hopping towards the nest. They usually departed from the nest directly, not via the nest tree.

The female recessed to defecate, to be fed by the male, to forage, and to perform other activities. Both sexes often wing-flicked in vicinity of the nest, and the female bill-wiped on branches while approaching the nest. The female sometimes recessed only to defecate copious white feces, which she did in the nest tree or from nearby vegetation; she then returned immediately to the nest. The male usually consorted with the female when she recessed and was observed feeding her during recesses, either in the nest tree or in nearby vegetation.

The female was fed by the male both on or off the nest. She solicited feeding by wing-fluttering or -quivering, and rarely by vocalizations audible to observers. At nest #2, we observed these feedings in better detail during the chick stage: when on the nest and anticipating the male's approach, she would point her bill up and begin bill-clapping with increasing frequency as the male neared. She was rarely heard giving a faint two-note call prior to the male's arrival, but this vocalization was hard to hear and could have gone unnoticed most of the time. All observations of food transferal were of regurgitation rather than of carrying and transferring food in the bill. The male delivered boli of food into the female's gaping mouth in the same way that he later fed the chicks. During feedings, the male perched on the same level or above or below her. The female often left the nest shortly before or as the male approached; by what cues she detected his approach are not known, perhaps by sight or by faint chit-chit calls rarely heard by us. We believe that the male fed the female during most recesses, because recesses were usually too short for the female to forage profitably and because on many brief recesses the male and female were seen consorting in dense cover, where they could not be further observed.

During the egg stage, the male was usually seen visiting the vicinity of the nest before or during the female's recesses or when he fed the

female on the nest. Twice, he chased the female in the nest tree. During a heavy rain he loafed, preened, and head-scratched under the shelter of a branch in the nest tree. Though he sometimes foraged in the vicinity of the nest tree, his usual long absences followed by his arrival and immediate feeding of the female suggest that he foraged mostly beyond view of the nest.

Nestling stage—parental behavior.—We observed nest #1 for 46.2 h during seven days and nest #2 for 66 h during 11 days of the nestling stage. We believe we observed hatching at both nests. At nest #1, we first saw a chick on 1 April. However, we suspect hatching occurred much earlier, perhaps on 25 March, when at 11:44, the female, incubating but fidgeting, hopped onto the nest rim and extracted from the nest cup a "flesh-colored object" 4 cm long and "flaccid," which she immediately consumed. The observer questioned whether she had eaten one of her own eggs. We doubt that the object was a hatched eggshell, because it didn't look like one, and other honeycreepers discard shells away from the nest (T. Pratt, pers. obs.). We also doubt it was a food item, because the female's last feeding was 17 min earlier, or a fecal sac of a small chick. Also, from that day onward, we noted that the female more frequently directed her attention to the interior of the nest. We assume that the observer had witnessed the female eating the contents of a broken egg or a dead chick.

At nest #2, the first hatching probably occurred on 11 May. The day previous, the female incubated uneventfully. On the morning of 11 May, she frequently interrupted incubation and directed her attention to the nest interior, and for the first time the male was seen checking the contents of the nest. Based on the parents' behavior, we believe that hatching occurred at about 10:00. At 11:02, the female may have fed a chick, and by the end of the day one definite feeding was observed. The second chick may have hatched on 13 May. On four occasions from 09:45 to 11:40 on 13 May, the female flicked objects that looked like eggshells (or fecal sacs?) from the nest. Afterwards, the male and female were observed simultaneously feeding chicks at two locations in the nest. We first observed a chick on 19 May. We could not determine the initial brood size at either nest, but observed only one chick at nest #1 and two chicks at nest #2, once the chicks began to lift their head above the nest rim.

Only the female brooded. Behaviors of the female at the nest were similar between the egg and nestling stages, but now included a behavior we call "nest-treading," feeding and grooming the chicks, nest sanitation and maintenance, drinking water drops from twigs, and an occasional brief nap. Nest-treading involved the brooding female treading the floor and inside walls, perhaps either to adjust her position and the chick's or

to stretch and enlarge the nest cup. The female fed the chicks with food she had collected herself, but more often with food given to her by the male at or away from the nest. Both parents carried food internally, rather than in their beak. However, during the old chick stage, food was sometimes carried in the beak. Fecal sacs were eaten, flicked over the side of the nest, carried and discarded away from the nest, or transferred from the female at the nest to the male to take away. Nest sanitation must have been efficient, because feces were not observed on the rim of the nests or found when the nests were collected. Behaviors of the female on recess did not change between the egg and nestling stages, except that in addition she discarded fecal sacs.

The male continued the same patterns of activity as during the egg stage. Though he fed the female on nest #1, he was not observed feeding or tending the nestling. Absence of observed care-giving by the male towards the chick at nest #1 may have been due to difficulty in viewing that nest, rather than an absence of such behavior. At nest #2, beginning on hatching day, the male frequently fed the female and nestlings and removed fecal sacs. On the day prior to fledging, the male on a few occasions delivered food to the nest by carrying a succineid snail in his mouth rather than internally.

Nestling stage—chick development.—Chicks remained huddled under their mother throughout the first two weeks in the nest and were usually seen only when they lifted their heads to feed. At nests #1 and #2, chicks were first seen, begging, on 2 April and 19 and 21 May (observers absent 15–18 May), respectively, when each attained nine days of age. Our data on the behavior of older nestlings is sketchy because chicks were observed for only three days during their last week in the nest. Nest #1 failed in a downpour of 350 mm rain during 8–14 April. Nest #2 fledged one chick on 31 May; fledging may have been delayed by weather, which was poor the day before fledging. The smaller and by then much weaker chick was last seen gaping on 29 May and is presumed to have died in the nest, though its remains were never found. In the two days prior to fledging, the surviving chick, when unattended, spent most of its time resting, preening, exercising in short bouts of wing-flapping, and drinking water off plant material. When fed, it flapped its wings vigorously. We never heard it call. Besides relying on its parents for nest sanitation, the chick also defecated over the side of the nest.

On 31 May, the day it fledged, the chick made several excursions to branches in the immediate vicinity of the nest, at first returning to the nest to be fed, then leaving the nest for feeding. It was first heard giving single, infrequent chip notes. Though the female brooded the chick on five occasions, the chick sometimes resisted by pushing her off the nest.
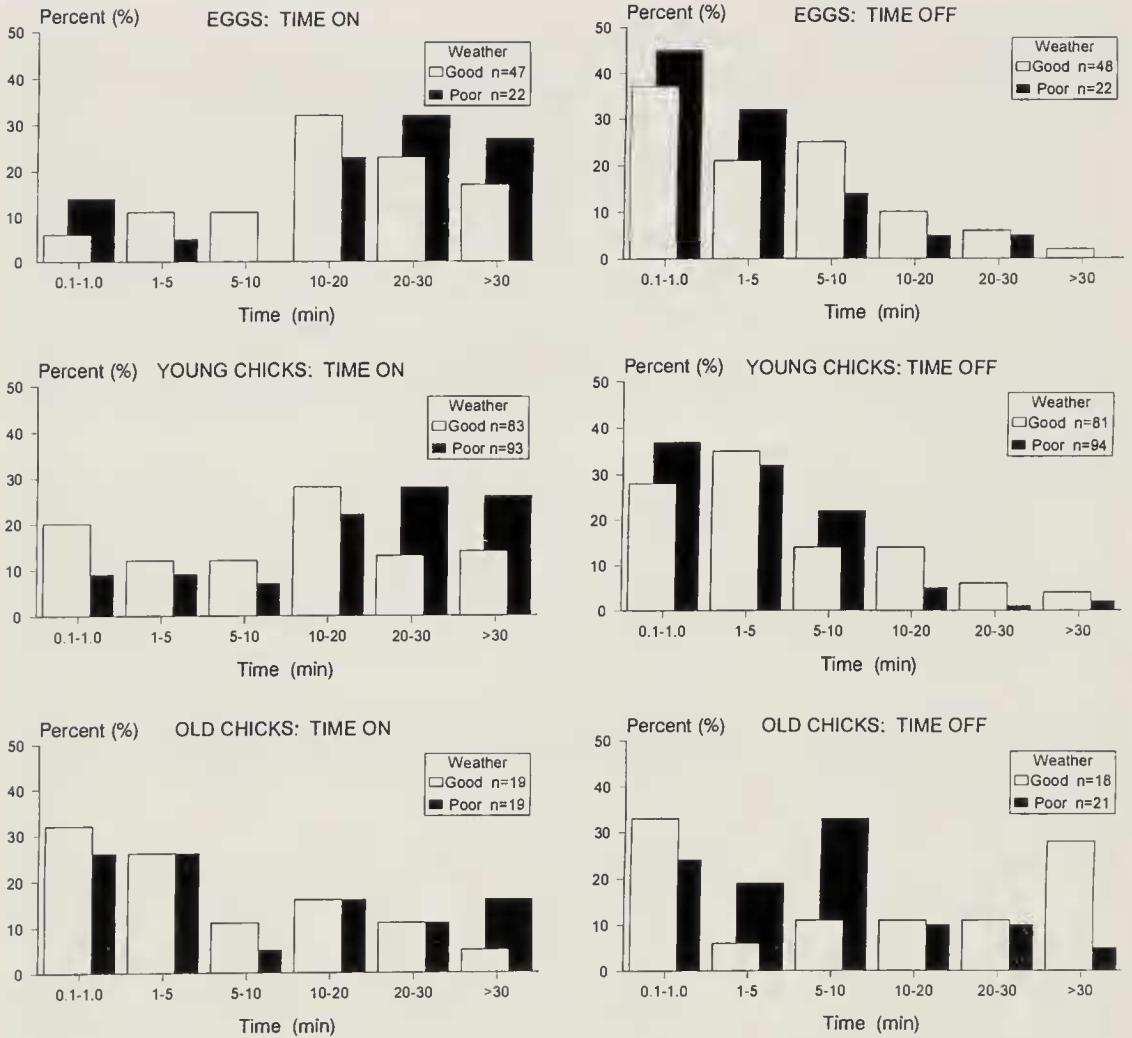
FIG. 1.   Frequency distribution (percent observations) of incubation, brood, and recess times of the female Poo-uli in good vs poor weather at nests #1 and #2 combined. Poor weather had winds >8 km·h^{-1} or rain or both. Shown are times for three stages: eggs, young chicks ($<$14 days old) and old nestlings ($\geq$14 days).

Shortly after 16:30, the chick fledged and moved into the canopy of the nest tree. It was 21 days old.

Fledgling stage.—We observed the parents attending the fledgling during 09:00–12:54 on 1 June. The fledgling was located in a 7 m tall pukiawe tree near the nest tree. It seemed to be alone, loafed most of the time, and remained in the subcanopy. It was capable of short horizontal flights. Both parents provided food. Though the parents occasionally gave chit-chit calls, the chick could not be heard. It wing-quivered while begging and moved about awkwardly.

Rates of incubation, brooding, and feeding.—Weather affected time spent on and off the nest by the female during the egg and young chick ($<$14 days old) stages (Fig. 1, Table 2). The female at nest #1 spent more

TABLE 2
Time (min) Spent by the female Poo-uli on and off the Nests in Good vs Poor (Winds > 8 km-h^{-1} or Rain or Both) Weather during Stages of Eggs, Young Chicks (<14 Days Old), and Old Chicks (≥14 Days Old)

| | | Nest #1 | | | | | | Nest #2 | | | | |
| | | Time on | | | Time off | | | Time on | | | Time off | |
Stage	Weather	N	Mean	SE	Mean	SE	N	Mean	SE	Mean	SE
Egg	Good	41	14.5	2.25	6.3	1.25	18	25.0	2.12	7.7	3.05
	Poor	18	25.1	7.43	4.2	2.25	11	24.9	4.38	3.9	1.24
Young chick	Good	51	15.2	1.63	2.7	0.46	47	12.4	2.19	11.5	1.79
	Poor	62	21.0	2.17	1.7	0.30	53	25.9	3.02	8.2	1.43
Old chick	Good						19	7.9	2.41	18.2 .	5.18
	Poor						25	11.2	3.04	8.6	2.09

time on the nest during poor weather (mean ± SD = 21.8 ± 17.6 min) than during good weather (14.9 ± 11.5 min; two-way ANOVA, $F_{2,132}$ = 3.91, P = 0.02). Nest stage (eggs vs young chicks) did not significantly affect time spent on the nest for nest #1 ($F_{1,132}$ = 0.34, P = 0.56), but the length of recesses was longer when the female was incubating (5.7 ± 7.3; $F_{1,137}$ = 12.02, P = 0.0007) than when she was brooding young chicks (2.2 ± 2.7 min). Length of recesses at nest #1 was 4.2 ± 5.33 min during good weather and 2.2 ± 4.11 min during poor weather, but was highly variable ($F_{2,137}$ = 2.34, P = 0.10).

For nest #2, nest stage and weather affected both time on the nest (two-way ANOVA, $F_{6,137}$ = 5.86, P = 0.0001) and time off the nest ($F_{6,135}$ = 2.11, P = 0.056). Time spent on the nest (mean ± SD) was 25.0 ± 10.1 min for egg, 19.5 ± 18.4 min for young chick, and 9.5 ± 11.9 min for old chick (≥14 days old) stages. Pairwise comparisons of means showed that differences were not significant between egg and young chick stages, but significant for young chick and old chick stages (Tukey's test, P < 0.05). Mean time spent on the nest was 14.1 ± 13.1 min during good weather and 21.8 ± 18.5 min during poor weather. Mean length of recesses was 6.4 ± 10.5 min for egg, 9.7 ± 10.0 min for young chick, and 13.0 ± 17.0 min for old chick stages. None of the pairwise comparisons of means was significant (Tukey's test, P < 0.05). Recess time was 12.4 ± 15.3 min during good weather and 7.8 ± 8.8 min during poor weather, again highly variable.

The daily rate at which the male fed the female while she was on the nest was not statistically different between good and poor weather during both the egg stage (0.23 vs 0.66 feedings·h^{-1}; 22.0 and 12.1 h, respec-

TABLE 3

NUMBERS OF IDENTIFIED FOOD ITEMS TRANSFERRED FROM MALE TO FEMALE OR FROM ADULTS TO CHICKS AT NEST #2

Chick age[a]	Number of feedings	Cater-pillars	Pale larvae	Succineid snails	Other snails	Beetles	Total
1–4	8	6+	3	0	(8?)	0	9 or 17
10–12	12	17	9	(2?)	0	0	26 or 28
19–21	32	30	17	34	4	1	86

[a] Age of the oldest chick in days.

tively; $Z = 1.687$, $P = 0.091$) and the young chick stage (1.08 vs 0.95 feedings·h^{-1}; 30.5 and 49.5 h, respectively; $Z = 0.556$, $P = 0.582$). Rates of the male feeding the female increased significantly from the egg to young chick stage (0.38 vs 1.00 feedings·h^{-1} incubation or brooding; 34.1 and 79.9 h, respectively; $Z = 4.03$, $P = 0.0001$), because the male's main purpose for visiting the nest was to feed the chicks directly or via the female. During the old chick stage, the female spent little time on the nest, and consequently there were few male-to-female feedings.

Feeding rates of chicks varied with sex of parent and weather at nest #2. The female fed young chicks at a significantly greater rate than did the male (1.77 vs 1.03 feedings·h^{-1}, 43.6 h observation; $Z = 2.920$, $P = 0.004$); however, the increased male-to-female feedings were likely passed on to the chicks by the female, so that the male's role in providing food to young chicks could have been the same or greater than the female's. For older chicks, feeding rates by female vs male showed no significant difference, perhaps due to small sample size (1.60 vs 2.24 feedings·h^{-1} in 15.6 h; $Z = 1.290$, $P = 0.197$). Parents fed young chicks more often in good than in poor weather (1.95 vs 1.04 feedings·h^{-1} in 17.2 and 26.5 h; $Z = 3.257$, $P = 0.001$); data were insufficient for old chicks.

Diet.—We cannot state whether items identified represent the complete diet, because we could not view or identify most food transferred, and in cases when we did recognize food items, these were only one or a few items in each transfer. Most food appeared as indeterminate goop. Most food items identified were lepidoptera and coleoptera larvae (Table 3). Molluscs did not appear for certain in the food until the chick was near fledging, when succineids became an important dietary component.

Interspecific interactions.—The Poo-uli did not actively defend their nests from approaches by other honeycreepers. We recorded 14 approaches to within 2 m of nest #1: 11 by Apapane (*Himatione sanguinea*), 1 by either an Apapane or Iiwi (*Vestiaria coccinea*), 1 by a Common Amakihi (*Hemignathus virens*), and 1 by a Maui Alauahio (*Paroreomyza mon-*

tana). In nine approaches, the female was incubating or brooding and did not respond, apart from watching the intruder or crouching lower in the nest. In two of five instances when the female was off the nest and an intruder approached, the male or female drove the intruder (Apapane) away with displays and chasing. When displaying, the Poo-uli crouched and, with neck extended forward, faced the intruder. In both instances, we believe the nest was at the egg stage. On 14 April, after nest #1 was abandoned, Apapane entered it several times, presumably collecting nesting material. Apapane gather building material from nests of other birds (Eddinger 1970).

Vocalizations

When not breeding, Poo-uli vocalize infrequently (Engilis 1990, Mountainspring et al. 1990). Their calls are inconspicuous and very simple in structure, consisting mainly of chit (chip, whit, or tch) notes given singly, in couplets, or in short bursts (see Pratt 1992 for sonogram). Vocalizations given while nesting are similarly rare and quiet.

Song.—A single male song on 5 March initially alerted us to a possible nest; yet, only one song was heard from 13:15 to 16:35. Songs were heard more frequently on 6 March when nest #1 was still under construction, twice on 17 March early in the egg stage, and not at all later. The male's song consisted mainly of paired couplets in iambic pattern speeding up towards the end and was audible only within 40 m of the bird. The following song heard during courtship at 13:45–13:50 on 6 March was typical: "Chit-chit chit-d chit-ter chit (pause) chit-ter chit-ter chit-ter."

"Chit-Chit" call.—One to many notes; usually two repeated. Frequently given by male or female during construction of both nests and on three occasions by the male during the chick stage at nest #2 when he accompanied the female on recess. On three occasions on 10 and 12 May, the male gave chit-chit calls shortly before the female left the nest to join him. The female gave soft chit-chit calls as he approached nest #2 on 20, 21 May.

Chit notes.—Single "chit" notes were given by parents while foraging together, perhaps as an interspecific flocking call, similar to that of Maui Alauahio.

Alarm call.—During the nestling stage on 2 April at 16:32, the male gave a series of three-noted calls, "chit, chit, chit," interspersed between bouts by single "chit" notes. He was seen perched low in a *Myrsine* sp. tree, while the female brooded. Observers wrote that he "was most likely disturbed by something and giving vocalizations to ward it off," and they implied that the something may have been a small mammal.

Whistle call.—Given once (7 April) by the male foraging in heavy rain

in the vicinity of the brooding female at nest #1 and given on four oc-
casions (14 April) by the male during construction stage of nest #2.

Chatter.—Once during the egg stage at nest #1, the female gave four
note chatter while wing-quivering and being fed by the male 1.5 m from
the nest. Another observer believed that the male gave the chatter call
during feeding.

Nestling calls.—These, if any, were inaudible from the observation
points. On the day the successful chick fledged, it gave single, infrequent
chit notes when alone on the nest.

Fledgling calls.—We heard none. Reynolds and Snetsinger (pers.
comm.) described the calls of a juvenile Poo-uli being fed on 30 August
1994 as "a high-pitched rapid twitter very similar to that of a juvenile
Hawaii Creeper (*Oreomystis mana*) or Hawaii Akepa (*Loxops coccineus
coccineus*) being fed."

Mechanical sounds.—None. Flight was silent, lacking the wing-whir
of some other Hawaiian honeycreepers.

DISCUSSION

Nest site.—The two nest sites we studied are important from both an
evolutionary and conservation perspective. Why did the Poo-uli build
their nests in tall ohia lehua? Poo-uli forage in the understory and sub-
canopy at a modal height of 5 m (Mountainspring et al. 1990); the two
nests at 8 m were at the high end of their reported foraging range. Even
more puzzling, why do the other six species of honeycreepers in Maui
rain forests also nest almost exclusively in canopy ohia lehua? Given (1)
the diversity in morphology, behavior, and life history traits evolved by
the Hawaiian honeycreepers (Amadon 1950, Freed et al. 1987) and (2)
the diversity of nest sites used by continental fringillids (Bent et al. 1968,
Newton 1972) and passerine communities generally (Martin 1988), the
uniformity in nest site selection by rain forest drepanidines is unexpected.
While it is beyond the scope of our paper to explore this convergence in
the selection of nest sites, we call attention to historic changes in pre-
dation pressure on nesting birds in Hawaii. Prior to human settlement, all
potential nest predators in these insular forests were birds—rallids, ibises,
raptors, owls, corvids, and drepanidines. Nearly all have vanished from
Maui forests, and instead six species of small mammals have invaded—
a mongoose (*Herpestes auropunctatus*), a cat (*Felis catus*), and four ro-
dents (*Mus musculus, Rattus exulans, R. norvegicus, R. rattus*). Most hon-
eycreeper species have become extinct as direct and indirect consequence
of human settlement, including mammalian predation; the surviving spe-
cies may be nesting in sites relatively safe from the new predators.

Breeding system and parental care.—We have no evidence to show

that the Poo-uli defended an all-purpose territory, as no other conspecifics were seen during the study, and the male did not sing to advertise a territory. Nor did either parent consistently defend the nests from approach by other species. Sightings of the parents foraging in the vicinity of the nest, their relatively weak flight, and the absence of long flights over the canopy suggest that the pair may have confined their activity to a home range of only a few hundred meters in radius.

Even with a sample size of one pair, we are tempted to infer that Poo-uli are principally monogamous, because of the heavy involvement of the male at all stages of the nesting cycle. Pair-bonding extends at least through the breeding season, for the pair initiated the second nest with minimal courtship and no singing. The pair bond may have been reinforced by the male feeding the female regularly throughout both nesting cycles and by the pair consorting during the female's recesses from the nest. Monogamy is universal among drepanidines studied to date (Eddinger 1970; van Riper 1980, 1987; Pletschet and Kelly 1990; Morin 1992; H. Baker and P. Baker, pers. comm.; T. Pratt, unpubl. data; J. Simon, pers. comm., E. van Gelder, pers. comm.) and carduelines generally (Newton 1972).

Parental care by the male and female resembled that of nine other drepanidines studied to date and of carduelines generally (Eddinger 1970; Newton 1972; van Riper 1980, 1987; Pletschet and Kelly 1990; Morin 1992; H. Baker and P. Baker, pers. comm.; T. Pratt, unpubl. data; J. Simon, pers. comm.; E. van Gelder, pers. comm.). We note the likely increase of care-giving to older chicks by the male, documented in few other drepanidines (Morin 1992), but perhaps common. Both parents performed nest sanitation throughout the nestling phase, and we found the successful nest #2 clean of feces. Among drepanidines studied to date (Eddinger 1970; Newton 1972; van Riper 1980, 1987; Pletschet and Kelly 1990; Morin 1992; H. Baker and P. Baker, pers. comm.; T. Pratt, unpubl. data; J. Simon, pers. comm.; van Gelder, pers. comm.), only the Laysan Finch (*Telespiza cantans*) and Palila (*Loxioides bailleui*) give up nest sanitation in the final week of the nestling stage, allowing the rim of the nest to become heavily encrusted with feces. Complete (or nearly complete) nest sanitation by the Poo-uli and other drepanidines that feed their young principally on invertebrate rather than plant foods is presumably a derived behavior, as other carduelines are less fastidious (Newton 1972). The seasonal span of the two Poo-uli nests coincides with peak nesting for most other drepanidines in Maui rainforests (H. Baker and P. Baker, pers. comm.; J. Simon, pers. comm.; E. van Gelder, pers. comm.) and on other islands (Eddinger 1970, Ralph and Fancy 1994).

The male Poo-uli's role of provisioning food to the nesting female and

to his chicks assumes added importance in climatic conditions on the species' relictual geographic range. New weather stations in Poo-uli habitat have recorded annual rainfall ranging from 5–12 m (L. Loope, pers. comm.). Here, trade wind showers can prevail for weeks. Poor weather can threaten the eggs and chicks with hypothermia and pit the survival of progeny against that of parents faced with constraints on foraging time (Drent 1975). Poor weather delayed the female Poo-uli from leaving the nest and curtailed her recesses for foraging. Reduced foraging by the female may have been compensated with provisioning by the male who continued to feed the female on the nest at the same rate (feeding bouts per time spent by the female on the nest) in poor weather as in good. However, the rate at which parents fed the young chick decreased from good to poor weather. We note the greater importance of wind versus rain in influencing the female Poo-uli's time on and off the nest. Wind can have a severe effect on egg temperature, incubation, and incubation behavior in small passerines (e.g., Morton and Pereyra 1985). However, we believe that rain could have had a much greater effect on parental behavior than measured by us. Heavy rains prevented us from observing the nests, and this biased our sampling to "drier" conditions. For example, we were unable to observe nest #1 through the curtain of rain that may have caused its failure. Lastly, Cartar and Montgomerie (1987) found that for female White-rumped Sandpipers (*Calidris fuscicollis*) incubation "behavior appears at least to integrate the effects of both present weather and weather on the previous day." We could not explore such effects with the Poo-uli because of our small data set.

Skutch (1976) noted that time spent on the nest was greater for species in which the incubating bird received food from its mate. He also pointed out the influence of rain on nesting birds. The slower growth rates of chicks of tropical birds has been attributed to food limitation via reduced rate of food delivery by parents (Ricklefs 1976, Martin 1987). The adaptive advantage of monogamous male birds provisioning their mate and young in windy and/or high rainfall environments has received little attention.

Chick development.—The nestling period of 21 days for our Poo-uli chick is intermediate between 15–21 days for Common Amakihi (van Riper 1987) and 22–26 days and 23–29 for Laysan Finch (Morin 1992) and Palila (van Riper 1980; Pletschet and Kelly 1990; T. Pratt, unpubl. data), respectively. At 25.5 g (N = 1; Engilis et al. 1996), the mass of the Poo-uli is greater than that of the Common Amakihi but smaller than that of the Laysan Finch and Palila, suggesting an intermediate nestling period. Nestlings of European cardueline finches that nest in low bushes spend fewer days in the nest and leave at an earlier stage of development

than do nestlings of carduelines nesting in tall shrubs and trees (Newton 1972). Newton (1972) considered early fledging as an adaptation miti- gating greater risk to predation. Nestling stage for all four drepanidines is longer than that for shrub- or tree-nesting carduelines (Newton 1972). However, the drepanidine chicks fledged at an advanced stage of devel- opment, capable of level flight for short distances and with flight feathers and body size close to that of an adult (van Riper 1980, 1987; Pletschet and Kelly 1990; Morin 1992; T. Pratt, unpubl. data). These differences in fledging time and development indicate an advantage for a prolonged nestling period for the Poo-uli, and perhaps other drepanidines in montane Hawaiian ecosystems.

The second chick apparently hatched two days after the first chick, suggesting hatching asynchrony. The smaller chick died before the larger one fledged, suggesting brood reduction. Whether this is a pattern for second clutches in Poo-uli remains to be determined. Hatching asyn- chrony and brood reduction occur in Common Amakihi, Laysan Finch, and Palila (van Riper 1987; Pletschet and Kelly 1990; Morin 1992; T. Pratt, unpubl. data).

Diet.—Data on Poo-uli diet are few and tantalizing. Baldwin and Casey (1983), after painstaking analysis of stomach contents of the only two specimens, proposed that Poo-uli feed primarily on various small native lands snails (especially Succineidae), beetles, and proportionately few oth- er arthropods. Mountainspring et al. (1990) reported observations of Poo- uli feeding on insect larvae and succineid snails; they postulated that insect larvae might be a dietary component more important than proposed by Baldwin and Casey. If our data are representative, which they may not be because of observational bias, we confirm that Poo-uli feed exten- sively on succineid snails. However, we observed lepidoptera and cole- optera larvae being fed to nestlings at any age in greater proportion than succineid snails. Poo-uli appear to conform with most passerines by feed- ing caterpillars and other insect larvae to their young.

Vocalizations.—Our data, corroborated by observations of others (Mountainspring et al. 1990), show Poo-uli to be the quietest of all dre- panidines. We heard the male sing only during courtship and construction at nest #1. At the time of our study, Poo-uli densities were very low, and we did not observe this focal pair interacting with conspecifics. How greater population densities and encounters among birds affected rates of vocalizations is unknown. The song and chit-chit call are both diagnostic and useful for detecting Poo-uli. However, the species' rarity and infre- quent vocalizing render conventional censusing ineffective (Scott et al. 1986).

Implications for recovery.—We found nothing in the nesting biology

of this pair of Poo-uli to indicate problems for reproduction or population recruitment. Of significance may be the birds' placing their nests in the foliage of tall ohia lehua trees. We presume this location to be less hazardous than sites in tree cavities, subcanopy trees and shrubs, or near or on the ground, where nests might be encountered more often by non-native, mammalian nest predators. We observed *Rattus rattus* below the nest tree. This notorious enemy of insular birds (Atkinson 1985) thrives in high population density in the study area (Sugihara, in press). Whether the nest sites we observed are typical remains to be determined. Other factors that may help prevent detection of Poo-uli nests by mammalian predators are (1) complete nest sanitation; (2) the absence of odor at the nests, relative to other drepanidine nests (Pratt 1992); and (3) infrequent vocalizations at the nest. Nevertheless, we emphasize that reduction of small mammal populations is crucial to lessening the threat of nest predation for the Poo-uli (Kepler et al. 1984).

The long nestling period and the potential of no more than two young fledging would seem to handicap Poo-uli. However, Maui Alauahio and Maui Parrotbill (*Pseudonestor xanthophrys*), two other sympatric insectivorous honeycreepers sharing these life history characteristics and the same windy and rainy habitat, have far larger geographic ranges and population sizes. We suspect that factors such as decreasing food availability, habitat disturbance by feral pigs, and predation by non-native mammals may be more important to the Poo-uli's decline than vulnerability arising from the species' nesting behavior.

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